Conservation value of disturbed and secondary forests for ferns and lycophytes along an elevational gradient in Mexico

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Abstract: Questions: How do species richness and composition of fern assemblages change with elevation and, within elevational belts, in differently impacted forest habitats? Is there a relationship between fern assemblages and microclimate, both along gradients of elevation and disturbance? Which species are most sensitive to habitat disturbance and microclimatic changes? Location: The transect starts at sea level close to the Gulf of Mexico and ends 81 km away in a direct line on the eastern slopes of the Cofre de Perote at 3500 m, in central Veracruz, Mexico. Methods: We studied the richness and composition of fern assemblages in 120 study plots at eight elevations at 20-3500 m in three forest types: natural forest (NF), disturbed forest (DF) subjected to timber extraction and grazing, and secondary forest (SF) regrown after total clearance 15-20 years ago. In addition, we measured microclimatic conditions in the three forest types at five elevations over a year. Results: Fern richness peaked in humid montane forests at mid-elevations and was low in the dryer habitats at the ends of the gradient. Humid montane forests were most sensitive to disturbance, showing increases in mean annual temperatures by about 1°C and reduction in relative air humidity by about 20% in DF and SF compared to NF. This went along with a reduction of fern species richness by 5-60% and marked changes in species composition. In contrast, drought-deciduous forests at low elevations and coniferous forests at high elevations already had low humidity and high light intensity in NF and were less affected by human impact: Their microclimatic conditions and fern assemblages did not change markedly in DF and SF. Conclusions: The conservation of much of the humidity-dependent biota (ferns and presumably also groups such as bryophytes and amphibians) in humid montane forests depends on the protection of natural fragments without human disturbance. In contrast, the naturally open forests at the ends of the gradient can be subjected to some exploitation while conserving much of their fern flora as long as a general forest structure is maintained.

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Abstract

Questions: How do species richness and composition of fern assemblages change with elevation and, within elevational belts, in differently impacted forest habitats? Is there a relationship between fern assemblages and microclimate, both along gradients of elevation and disturbance? Which species are most sensitive to habitat disturbance and microclimatic changes?
Location: The transect starts at sea level close to the Gulf of Mexico and ends 81 km away in a direct line on the eastern slopes of the Cofre de Perote at 3500 m, in central Veracruz, Mexico.
Methods: We studied the richness and composition of fern assemblages in 120 study plots at eight elevations at 20-3500 m in three forest types: natural forest (NF), disturbed forest (DF) subjected to timber extraction and grazing, and secondary forest (SF) regrown after total clearance 15-20 years ago. In addition, we measured microclimatic conditions in the three forest types at five elevations over a year.
Results: Fern richness peaked in humid montane forests at mid-elevations and was low in the dryer habitats at the ends of the gradient. Humid montane forests were most sensitive to disturbance, showing increases in mean annual temperatures by about 1°C and reduction in

relative air humidity by about 20% in DF and SF compared to NF. This went along with a reduction of fern species richness by 5-60% and marked changes in species composition. In contrast, drought-deciduous forests at low elevations and coniferous forests at high elevations already had low humidity and high light intensity in NF and were less affected by human impact: Their microclimatic conditions and fern assemblages did not change markedly in DF and SF. **Conclusions:** The conservation of much of the humidity-dependent biota (ferns and presumably also groups such as bryophytes and amphibians) in humid montane forests depends on the protection of natural fragments without human disturbance. In contrast, the naturally open forests at the ends of the gradient can be subjected to some exploitation while conserving much of their fern flora as long as a general forest structure is maintained.

Key words: humid montane forest, degraded forest, indicator species, mature forest, microclimatic changes, secondary forest

Nomenclature : Tropicos: www.tropicos.org

Abbreviations :
NF= Natural forest
DF= Disturbed forest
SF= Secondary forest

Introduction

Human impact is profoundly altering the ecosystems and their associated biodiversity across the globe (Gibson et al. 2011), yet little is known for some taxa and ecosystems such as ferns and tropical mountains. Ferns and lycophytes (henceforth for simplicity called ferns) are two major plant lineages with high richness and abundance in humid tropical montane forests across the globe, where they can comprise up to 19% of the diversity of vascular plants at local and regional scales (Whitmore et al. 1985; Gentry & Dodson 1987; Kessler 2001a; Kreft et al. 2010). Ferns are particularly suitable for studies on plant diversity and assemblage composition because of their cosmopolitan distribution with a high but manageable number of 10000-13000 species

globally (Moran 2008); the relative ease of recognition in the field (Mickel & Smith 2004); their spore dispersal which limits biotic interactions resulting in more direct relationships towards abiotic factors (Page 2002); and because they contain both taxa that are sensitive to habitat disturbance and those that are more resilient (Mehltreter 2008).

In tropical mountains, ferns generally show the highest richness at intermediate elevations of about 1500-2000 m, with strongly decreasing richness towards lower and higher elevations (Kessler 2001a; Kluge et al. 2006; Watkins et al. 2006a; Kessler et al. 2011; Salazar et al. 2015). Little is known about ferns in non-natural ecosystems, but some studies have documented losses in species richness of 40-70% in logged and secondary forests compared to natural forests (Paciencia & Prado 2005; Mehltreter 2008; Rodríguez-Romero et al. 2008; Haro-Carrión et al. 2009; Carvajal-Hernández et al. 2014). In contrast, a study in Bolivia has documented that slightly disturbed montane forests have more regionally endemic ferns than natural forests (Kessler 2001b). These previous studies have largely ignored two interesting themes: i) changes on the impact of human activities in relation to elevation and in different forest types (Kessler et al. 2001) and ii) changes in the diversity of ferns in the transition zone between the Neotropic, where ferns are very diverse (Salazar et al. 2015), and the less diverse transition zones between the Neotropic and Neartic, as it occurs in central Mexico (Sánchez-Colón et al. 2009). For example, the state of Veracruz, where our study was conducted, is home to 564 fern species (Tejero-Díez et al. 2014; Krömer et al. 2015) but has also lost in the last 30 years, 85% of its natural vegetation cover (Castillo-Campos et al. 2011). This has resulted not only in the outright conversion of forests to fields or pastures, but also in the creation of secondary forests and agroforests. Because of their dominance of trees, such ecosystems may play important roles in the conservation of forest-dependent biota (Dent & Wright 2009; Clough et al. 2011). However, they also differ in important ecological traits from natural forests, such as a lower abundance of large trees, as well as reduced shading that goes along with increasing temperatures and reduced air humidity (Scatena et al. 2005; Sporn et al. 2009). Such microhabitat changes are likely to affect especially humidity-dependent organisms such as ferns, but little is known about this. In particular, it has been suggested that the impact of human disturbance may differ between forest types depending on the water availability in the forests (mainly relative air humidity and rainfall) (Werner et al. 2005, 2011; Einzmann et al. 2016). Natural dry forests such as drought-deciduous forests found in many regions of Central America and the Andes, are defined as ecosystems with

a closed canopy, on fertile soils and precipitation less than 1800 mm per year, with prolonged droughts and a dominance of deciduous species (Banda et al. 2016). Therefore they are inhabited by species already adapted to water stress, so that alterations of the forest structure may not greatly affect the species richness (Carvajal-Hernández & Krömer 2015). In contrast, humid montane forests, especially those towards the aridity limit of this habitat, appear to be highly susceptible to alterations of forest structure that lead to major microclimatic changes (Sánchez-Ramos & Dirzo 2014).

In the present study, we set out to quantify the impact of human disturbance on the patterns of diversity and assemblage composition along an elevational gradient in central Veracruz, Mexico. This gradient covers a wide range of habitats, from semi-deciduous forests at low elevations, humid montane forests at intermediate elevations and coniferous forests at elevations above 3000 m. It contains also a mix of natural forest remnants, disturbed forests, and secondary forests. This thus allows comparing the influence of human impact in different ecosystems. The main questions of this study were: How do species richness and composition of fern assemblages change with elevation and, within each elevational belt, in differently impacted forest habitats? Is there a relationship between fern assemblages and microclimate, both along gradients of elevation and disturbance? Which species are most sensitive to habitat disturbance and microclimatic changes?

Materials and methods

Study area

Theelevational gradient forms part of the drainages of the rivers La Antigua in its higher part (within the Sierra Madre Oriental) and Actopan in the median and lower parts (in the Sierra de Manuel Díaz) (Fig. 1). The transect starts at sea level close to the Gulf of Mexico (19 35'N, 96°22'W) and ends 81 km away in a direct line on the eastern slopes of the Cofre de Perote at 3500 m (19°30' N, 97°08'W). Climate changes from dry-hot at low elevations (average annual temperature and total annual precipitation: 25° C/800 mm) to humid-temperate at mid-elevations (18° C/1800 mm) and dry-cold at high elevations (9° C/ 800 mm). While temperature decreases linearly with elevation, precipitation is highest in the middle of the gradient (Soto-Esparza & Giddings 2011). The natural vegetation combines elements of Nearctic and Neotropical affinities, with tropical oak forest below 1000 m, humid montane forests at 1500-2300 m,

transitional *Pinus-Quercus* forests at 2300-2700 m, and coniferous forests above 2800 m (Castillo-Campos et al. 2011). At most elevations, it is possible to find both remnants of the natural vegetation as well as disturbed forests and secondary forest resulting from clearcutting some 15-20 years ago, according to the comments of local people.

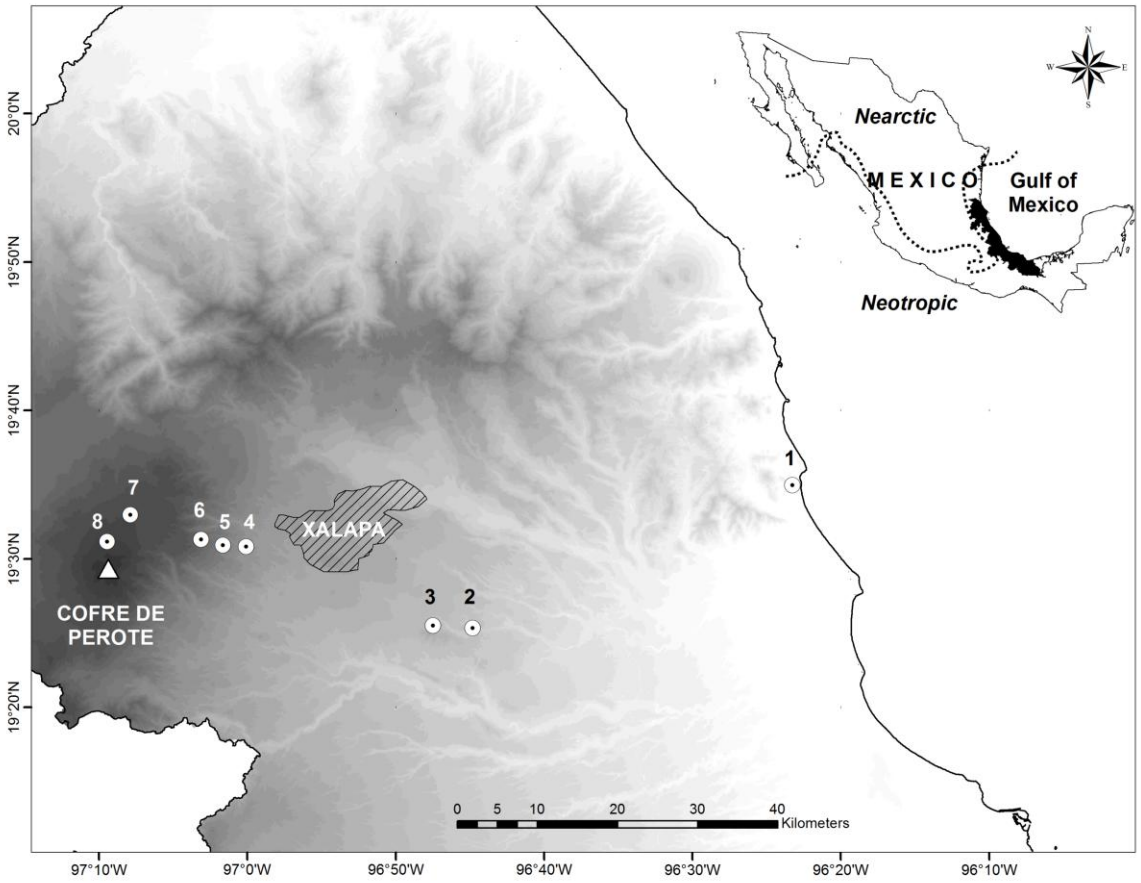

Fig. 1 Location of the eight study sites in Veracruz State, Mexico. 1. La Mancha (20 m); 2. Palmarejo (500 m); 3. Chavarrillo (1000 m); 4. Los Capulines (1600 m); 5. El Zapotal (2000 m); 6. El Encinal (2500 m); 7. Los Pescados (3000 m); El Conejo (3500 m).

Field work

From February 2012 to October 2013, we established 120 study plots at eight elevational belts, separated by about 500 m (Fig. 1), in three different habitats: i) natural forest (NF) not disturbed, ii) disturbed forest (DF) subjected to selective logging and grazing by goats or cattle, and iii)

secondary forests (SF) regenerating after clearcutting some 15-20 years ago, locally known as *acahuales* (Romero et al. 2000).

At each elevational belt, a systematic sampling was performed, which consisted in establishing 15 study plots of 20 x 20 m each (Kessler & Bach 1999), with five plots in each habitat (NF, DF, SF). In each plot, we recorded all terrestrial ferns and epiphytic ones (presence/absence) up to a height of about eight m (Krömer et al. 2007). The specimens collected were deposited in the National Herbarium (MEXU) of the Institute of Biology of the UNAM, Mexico City, as well as partially in the herbaria of the University of Veracruz (CIB), Xalapa, University of California (UC), Berkeley and / or the Institute of Ecology, A.C. (XAL), Xalapa.

We placed 42 microclimate data loggers (HOBO PRO v2) to record air temperature and relative humidity, as well as light intensity (HOBO Pendant Temperature/Light Data Logger) for one year (January to December 2014) every 30 minutes at five elevations (500 m, 1000 m, 1500 m, 2500 m, and 3500 m), which represent the five different types of vegetation present along the entire gradient; in all three habitats we placed two data loggers that recorded temperature and humidity and one that recorded light intensity (however, in 3500 m it was not possible to get the complete data due to a light intensity data logger failure). These were placed on tree trunks at 2-3 m above the ground. In addition, in all plots hemispherical photographs through a "fish eye" lens were taken to measure the canopy openness and transfer of light into the understory.

Data analyses

We used a nested ANOVA to test if there were differences in the species richness per plot along the elevational transect and with respect to the three habitat types, with a post hoc Tukey test. Similar analyses were then conducted for daily mean values of temperature, relative humidity, and light intensity. Moreover, a Spearman correlation was calculated between the values obtained by the data loggers and canopy openness and light transfer that were obtained from the hemispheric photographs.

We used Whitaker's index of beta diversity (Whitaker 1960; Koleff et al. 2003; Tuomisto 2010) to assess the turnover of species between different elevations and between the three different habitats in each of the elevational belts. We then used a generalized linear model (ANCOVA) to assess elevational and habitat-dependent differences in beta diversity (this comparison was made considering the species turnover from NF to DF and SF, as well from DF

to SF), using the program Infostat 2015 (Grupo InfoStat, FCA, Universidad Nacional de Córdoba, Argentina). To identify indicator species for the different habitats, we conducted IndVal analyses (Dufrêne & Legendre 1997) at each elevation using the package labdsv 1.5-0 in R (Development Core team; version 3.1.2).

Results

Species richness

In the 120 study plots, we recorded 155 species of ferns belonging to 62 genera and 24 families (information on taxonomic classification and a species list are available in Carvajal-Hernández & Krömer 2015). Species richness peaked at 1500 m (67 species in total in all 15 plots) and 2000 m (62 species), whereas plots at the ends of the gradient had much fewer species (four species at 20 m and six species at 3500 m) (Fig. 2). The forest type with maximum richness thus was the humid montane forest, followed by the transitional *Pinus-Quercus* forest (2500 m) and the semi-deciduous forest at 500 m.

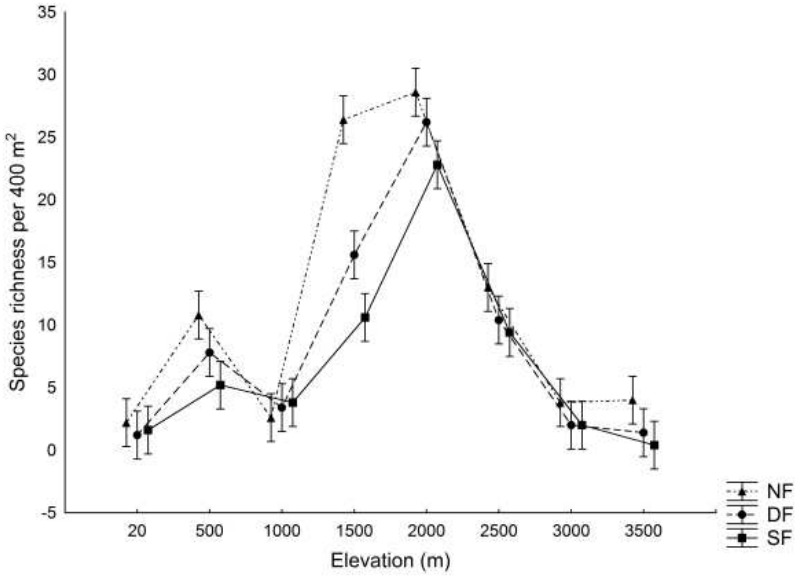

Fig. 2 Patterns of species richness in the three forest types (NF: natural forest; DF: disturbed forest; SF: secondary forest) at the eight study sites along the elevational gradient. For clarity of presentation, the values at a given elevation are slightly shifted in elevation.

In general, the middle part of the gradient had a significantly higher species richness per plot than the ends of the gradient (nested ANOVA, F=88.346; df=21; P<0.001). Disturbed (DF) and secondary forests (SF) had significantly fewer species than natural forest (NF) (nested ANOVA, F=44.189; df=2; P< 0.001). There was a significant interaction between elevation and habitat (nested ANOVA, F= 2084. 20; df=1; P=0.001) reflecting that at mid-elevations DF and SF only had 30-53% as many species per plot as NF, whereas at the ends of the gradient species richness per plot was roughly similar in all three forest types. According to the Tukey test, the comparison between DF and SF, indicates that there were no significant differences in the values of species richness in the middle zones of the gradient and even less at the ends of the elevational gradient.

Species turnover

Species turnover between plots in NF was fairly low (Whittaker's beta of, on average, 0.38±0.2). Turnover between plots in NF and those in DF was higher (0.50±0.23) and between NF and SF even higher (0.56±0.22). In general there was a negative linear relationship between the species turnover in different habitats as a function of elevation(ANCOVA, R=0.50; P<0.001) (Fig. 3). The generalised linear model showed that species turnover was influenced both by elevation (F=7.151; df= 4; P<0.001) and habitat type (F=8.825; df= 2; P< 0.001).

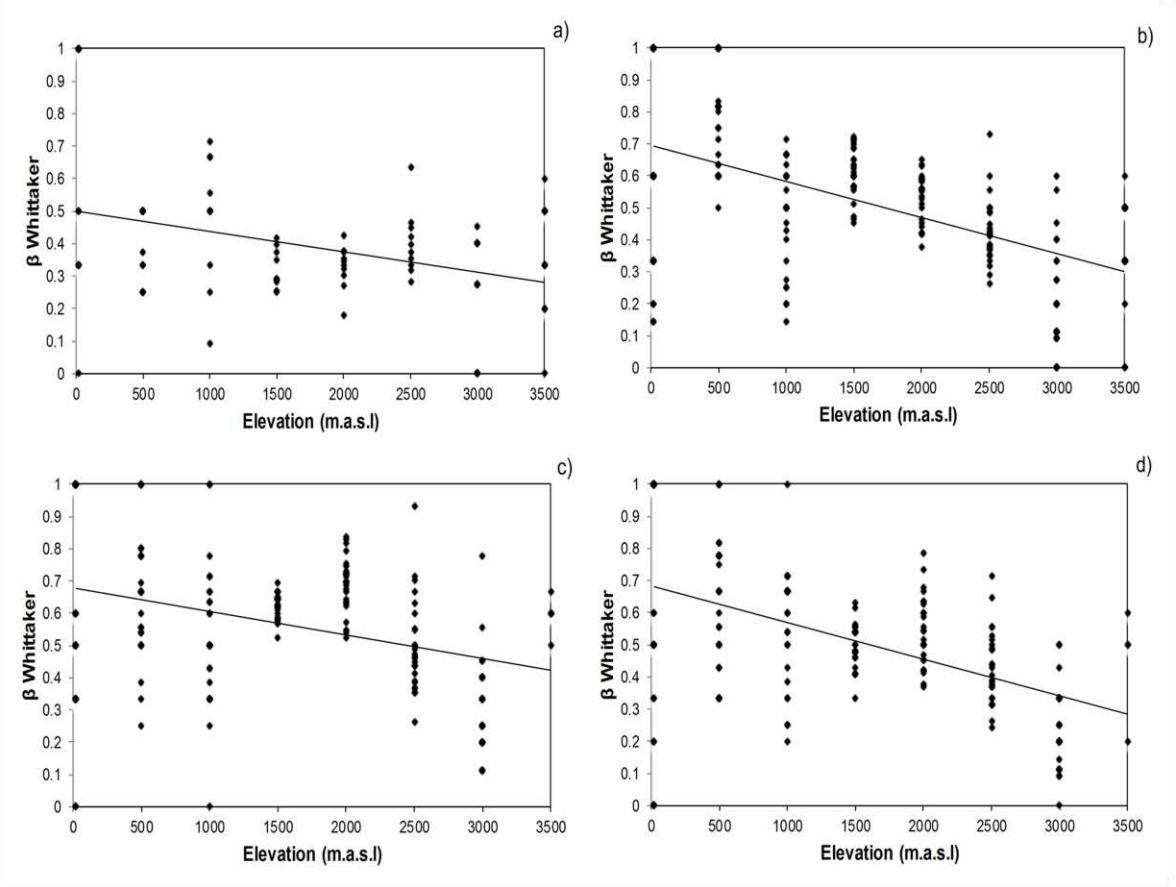

Fig. 3 Linear regression models of species turnover according to Whittaker's index (β_W) for the three forest types along the elevational gradient. a) NF-NF represents the comparison of plots in natural forest at a given elevation (r=-0.45; P<0.001); b) NF-DF between plots in NF and disturbed forest (r=-0.54; P<0.001); c) NF-SF between NF and secondary forest (r=-0.43; P<0.001); d) and DF-SF between disturbed forest and secondary forest plots (r=-0.51; P<0.001).

Microclimate

Temperature (nested ANOVA, F=2181.0; df: 12; P<0.001), relative air humidity (RH) (F=236.9; df: 12; P<0.001), and light intensity (F=209.9; df: 11; P<0.001) changed with elevation (Fig. 4). Also, there were significant differences in those microclimatic variables between the forest types at each elevational belt: temperature: F=32.7; df: 2; P<0.001; RH: F=74.1; df: 2; P<0.001; light intensity: F=814.4; df: 2; P<0.001. On average, SF had mean daily temperatures about 0.6°C higher than NF, except at the lower elevations (500 m and 1000 m) where differences were about 0.2°C. The temperature fluctuation between the highest value and the minimum varied according

to elevation, however, it showed that on average, SF presented the largest fluctuation (7.05º C), followed by NF (6.9° C) and finally the DF showed less fluctuation (6.2º C). RH declined from about 90% in NF to 69% in SF at intermediate elevations, whereas at the highest and lowest elevations these differences were only in the order of 2-4%. Light intensity was highest in SF, except at 1000 m, where it was similar in all forest types (Fig. 4). The values obtained by hemispheric photographs show that the most open canopy occurred in SF (24.8 %), followed by DF (17.69%) and NF (13.49%). An example of this occurs in middle elevations, where SF presents the largest canopy opening, therewe also found decreased relative humidity, increased temperature and light intensity. Along the elevational gradient we observed a negative correlation between canopy openness and the relative humidity and temperature; in contrast, the correlation is positive if the canopy openness is compared to the light intensity and transfer (Table 1).

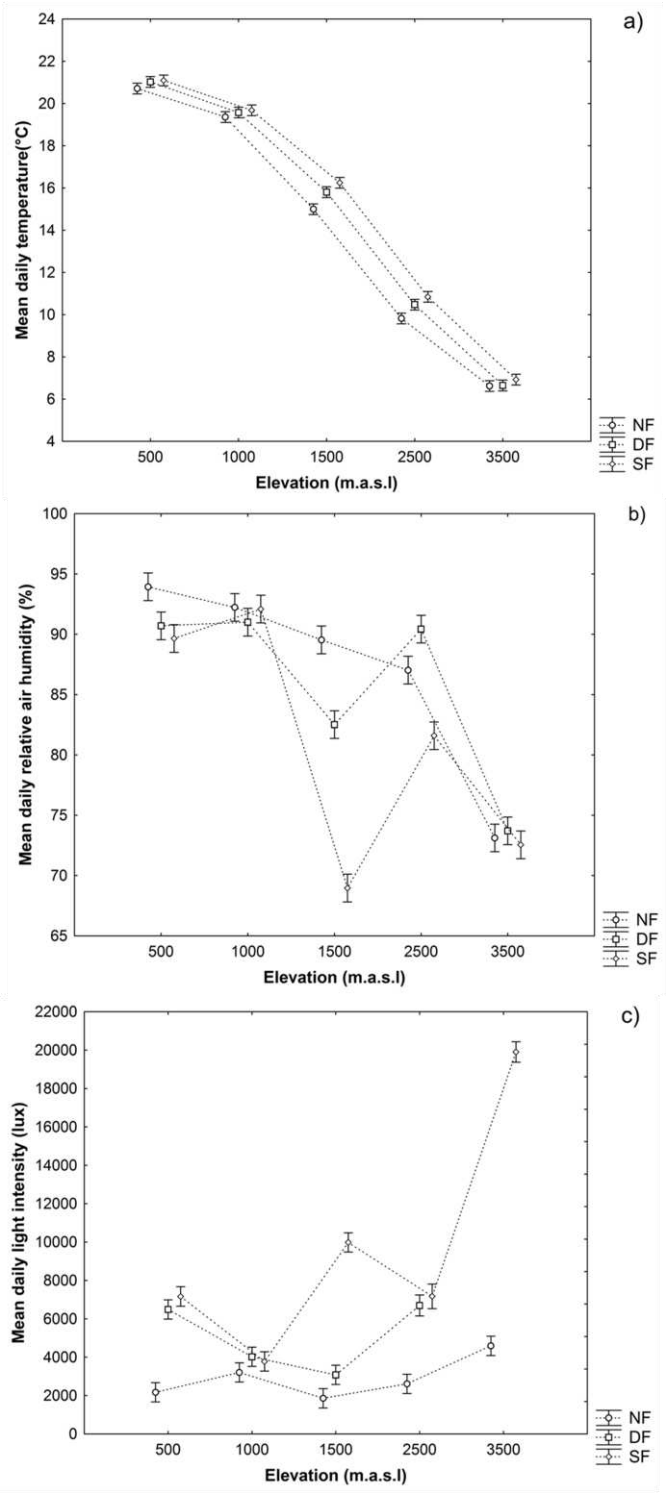

Fig. 4 Microclimatic conditions at five elevations along the study gradient, based on daily means over a year: a) Temperature; b) Relative air humidity; c) Light intensity. NF: natural forest; DF: disturbed forest; SF: secondary forest.

Indicator species

The IndVal analysis recovered 32 species significantly associated with specific forest types (Table 2). Of these, 23 (71.8%) were associated with NF, three (9.3%) with DF, and six (18.7%) with SF. Among the indicator species for NF were members of the Hymenophyllaceae family and groups such as the grammitid (Polypodiaceae) and vittarioid ferns (Pteridaceae), whereas in the disturbed habitats typical taxa included *Pteridium* (Dennstaedtiaceae) and *Thelypteris* (Thelypteridaceae). In the species-poor habitats at 20 m, 1000 m, and 3500 m, no indicator species were recovered.

Discussion

Species richness along the elevational gradient

The 155 fern species recorded in a total sampling area of only 4.8 hectare correspond to 27.5% of the 564 species currently known from the state of Veracruz and 15% of the 1030 species known from Mexico (Mickel & Smith 2004; Tejero-Díez et al. 2014; Krömer et al. 2015). While notable in a Mexican context, this richness is relatively low compared to other tropical areas, where up to three times as many species have been recorded in comparable surveys (Kessler 2001a; Kluge et al. 2006). This reflects the fairly abrupt reduction of fern species richness at the transition of the Neotropic to the Neartic (Kessler 2000; Moran 2008; Kessler et al. 2011; Carvajal-Hernández & Krömer 2015; Salazar et al. 2015).

Overall, the elevational species richness pattern found by us, with maximum richness at mid-elevations, is consistent with previous elevational studies in the tropics (Krömer et al. 2005; Kluge et al. 2006; Watkins et al. 2006a; Kessler et al. 2011). This pattern is usually interpreted as reflecting the physiological requirements of ferns for high humidity and moderate temperatures (Kreft et al. 2010; Kessler et al. 2011; Salazar et al. 2015), but although there are some studies that explain the physiological aspects of ferns (e.g., Watkins et al. 2006b; Brodribb & Mc Adam 2011; Shi-Bao et al. 2014), the mechanistic link between physiology and species richness is still unclear (Kessler et al. 2014).

A noteworthy departure from the overall pattern is the low richness at 1000 m. This cannot be attributed to low precipitation, since nearby data from climatic stations indicate that precipitation is intermediate between values recorded at 500 m and 1500 m (IMTA 2000) (For more information regarding precipitation data of the elevational gradient see Carvajal-Hernández

& Krömer 2015). However, the natural tree vegetation is also fairly species poor, being dominated by three species of *Quercus* (C.I. Carvajal, obs. pers.). A similar situation of low tree richness associated with low fern richness was found at 3000 m and 3500 m, where forests are formed by three species of *Pinus* and one of *Abies* (Ávila-Bello 2011; Castillo-Campos et al. 2011).

Yet, while low diversity at these elevations can be related to low temperatures and precipitation, no such simple environmental explanation is evident at 1000 m and contrasts with previous studies where richness values at 1000 m were intermediate between those at 500 m and 1500 m (Kluge et al. 2006; Watkins et al. 2006a). Interestingly, at this elevation, diversity recorded for the vascular flora in general is high (635 species), with 48 species of orchids, 44 Asteraceae, and 40 Fabaceae (Torres-Cantú 2013). In other regions in Mexico, and specifically in Veracruz, at this elevation some studies documented forests with a higher diversity of ferns. However, these were not considered in the present study because they are part of different physiographic regions, with different environments, substrates, wind exposure, and floristic composition (Carvajal-Hernández et al. 2014).

Human impact

At 500 m, 1500 m, 2000 m, and 2500 m, species richness of ferns was significantly reduced by 37-63% in disturbed (DF) and secondary forests (SF) compared to natural forest (NF). In tree plantations in humid montane forests within the study region, fern richness is even reduced by 70% relative to NF (Carvajal-Hernández et al. 2014). At these elevations, we also recorded high species turnover of 50-70% between NF on the one hand and DF and SF on the other. This was related to major changes in forest structure and accordingly in microclimate, with high light intensity and temperature conditions and lower relative air humidity (RH) in non-natural forests (Scatena et al. 2005; Zotz & Bader 2009). Although the temperature difference of about 1°C between NF and DF/SF recorded at 1500 m may appear to be minor, it is similar to an elevational difference of 200 m, which typically goes along with about 20% of species turnover (Kessler 2001b). It should be noted that the fluctuation between the maximum and minimum temperature was 7°C in SF. This difference throughout the day means that there are short periods of high temperatures that can be fatal for individuals of some species, such as epiphytes from the filmy fern family Hymenophyllaceae. The majority of the individuals of this family disappeared

in the areas subject to disturbance (Carvajal-Hernández & Krömer, 2015). Combined with air humidity reduced by about 20%, conditions were clearly quite different in the distinct forest types. It thus appears that humid montane forests, which have a dense, evergreen canopy and high cover of epiphytes are particularly susceptible to structural changes by human disturbance.

It should be noted that the DF retains less species richness than NF but does not differ statistically relative to richnes of SF. However, in terms of beta diversity, the species turnover between DF and SF is accentuated at medium and low elevations (Fig. 3). This indicates that the conditions of the DF affect some very sensitive species the NF. However, DF still conserves other primary species that in turn do not resist the most contrasting climatic conditions of SF. Therefore, in spite of the low number of species in DF, it represents an interesting reservoir of primary ferns that disappear when there is a more abrupt change in the habitat. This is probably related to the record of the lowest fluctuation in temperature, a situation that may be beneficial for some species. This is in accordance with the findings of Carvajal-Hernandez et al. (2014), who report that the stronger the disturbance, the greater is the loss of individuals of species.

The indicator species analysis recovered the highest number of species restricted or almost restricted to NF in humid montane forests. This included epiphytic species of filmy ferns (*Didymoglossum reptans, Hymenophyllum tegularis*, and *Polyphlebium capillaceum*), grammitid (Polypodiaceae) ferns such as *Terpsichore asplenifolia*, and vittarioid (Pteridaceae) ferns such as *Scoliosorus ensiformis* and *Vittaria gramminifolia*, as well as some large terrestrial species such as *Alsophila firma* (Cyatheaceae) and *Marattia laxa* (Marattiaceae). Several of these ferns have previously been identified as being particularly sensitive to changes in microclimatic conditions (filmy and grammitid fern groups) (Gehrig-Downie et al. 2013; Krömer et al. 2013). Filmy ferns, e.g., are known to require high air humidity for their survival and to be able to thrive under low light conditions, because the dwarfism tendencies combined with a hygrophilous biology, as their small fronds efficiently absorb water by diffusion on their filmy lamina (Dubuisson et al. 2003; Saldaña et al. 2014). In the case of *Alsophila firma*, a specialization has been demonstrated to wet environments (as NF) in the gametophytic phase (Riaño & Briones, 2015). In the case of vitariod ferns there are no specific studies on their ability to tolerate the changes in the habitat. In a previous study in central Veracruz comparing NF with agroforests, taxa that were especially susceptible to disturbance included the filmy ferns and the terrestrial genus *Phanerophlebia* (Dryopteridaceae) (Carvajal-Hernández et al. 2014).

At the ends of the gradient (20 m, 1000 m, 3000 m, and 3500 m), species loss in DF and SF was less pronounced at around 10%, and on occasion we even recorded slightly higher richness in disturbed forests. Accordingly, species turnover between NF and DF/SF was less pronounced at 20-30%. We consider that this may be related to the fact that at low elevations these forests are at least partly deciduous, so that even NF seasonally offers microclimatic conditions similar to forests used by humans. At high elevations, where forests are dominated by pines, vegetation structure is also quite open. In addition, pine forests appear to be generally unsuitable for ferns because of their dense litter layer of slowly decaying needles (van Wesenbeeck et al. 2003) and their thin branches with unstable bark that does not absorb much water, limiting their suitability for epiphytes (Callaway et al. 2002). For these reasons, fern species surviving at the ends of the study transect are already adapted to stressful environmental conditions and are thus less affected by human disturbance.

Concluding, our study shows that the fern assemblages of different forest types are susceptible to human disturbances to varying degrees. Humid montane forests in the study region appear to be strongly affected because of their naturally high humidity and low light availability, so that transformation of the forest structure leads to great changes in the microclimatic conditions (Larrea &Werner 2010; Carvajal-Hernández et al. 2014) that strongly affect the fern flora. The same may be assumed for other groups of organisms that depend on high air humidity such as bryophytes (Sporn et al. 2009; Zotz & Bader 2009) or amphibians (Vallan 2002). In contrast, the naturally open and comparatively dry forests at the ends of the gradient are inhabited by fern species already adapted to low air humidity and high insolation. Accordingly, they are less affected by forest disturbance. A similar situation has been documented in the Andes, where epiphytic plant assemblages of dry forests are less impacted by human disturbance than those of cloud forests (Werner et al. 2005; 2011).Our findings have important potential implications for tropical forest management and conservation. To adequately preserve the fern flora of humid montane forests in the study region, it is important to preserve natural fragments of this vegetation type without human intervention. In terms of species richness, DF and SF in this elevational belt are only of limited conservation value because their microclimatic conditions differ strongly from those of NF; however, considering the beta diversity among habitats, the DF is considered an important habitat for the conservation of species, specially in the intermediate zone of the elevational gradient where humid mountain forests are found. In contrast, in the more

open forests at the ends of the gradient, human use is at least partly compatible with the conservation of the associated fern flora, because as long as a forest-like vegetation structure is maintained, the microclimatic conditions are similar to those of the NF. In such a situation, extensive forest management is an appropriate strategy to ensure the survival of much of the forest biota. Additional studies from other regions and for other groups of organisms will be needed to confirm the generality of our conclusions, but considering the low cover of natural cloud forests that can be found in large parts of the Neotropics, their conservation in strict reserves without human use should clearly have the highest priority.

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Table 1 Correlation matrix of climatic variables in the three different habitats (natural forest, disturbed forest and secondary forest) along the elevational gradient at Cofre de Perote, Veracruz, Mexico.

	Canopy openness (%)	Relative air humidity (%)	Light intensity (lux)	Temperature (ºC)
Relative air humidity (%)	-0.24			
Light intensity (lux)	0.45	-0.38		
Temperature (ºC)	-0.14	0.300	-0.13	
Light transmission (%)	0.77	-0.34	0.50	-0.22

Table 2 Indicator species of the three forest types recovered in the IndVal analyses. NF: natural forest; DF: disturbed forest; SF: secondary forest. *IndVal values reflect affinity to a specific forest type, ranging from 1 (only recorded in that forest type) to 0 (not recorded).

Species	**Elevation (m)**	**Forest type**	**IndVal***	***p***
Adiantum andicola	500	NF	1	0.002
Alsophila firma	1500	NF	0.857	0.004
Asplenium harpeodes	1500/2000	NF	0.75/0.75	0.018/0.007
Blechnum falciforme	2000	SF	0.692	0.017
Blechnum wardiae	2000	NF	0.8	0.01
Campyloneurum amphostenon	2000	NF	0.7	0.032
Campyloneurum phyllitidis	500	NF	0.812	0.003
Cystopteris fragilis	3000	NF	0.476	0.028
Dicksonia sellowiana	2000	NF	0.9	0.002
Diplazium franconis	2000	NF	0.647	0.025
Diplazium striatum	2000	NF	0.8	0.006
Didymoglossum reptans	1500/2000	NF	0.8/0.8	0.012/0.009
Elaphoglossum sartorii	1500	NF	1	0.002
Elaphoglossum vestitum	1500	NF	0.833	0.003
Hymenophyllum tegularis	2000	NF	0.8	0.015
Lophosoria quadripinnata	2500	DF	0.515	0.006
Marattia laxa	1500/2000	NF	0.800/0.558	0.017/0.016
Pecluma sursumcurrens	1500	SF	0.592	0.041
Pleopeltis polylepis	2500	NF	0.777	0.004
Polyphlebium capillaceum	1500	NF	0.75	0.002
Polypodium conterminans	1500/2000	NF	0.746/0.642	0.010/0.015
Polypodium puberulum	1500/2000	SF	0.800/0.588	0.012/0.049
Pteridium aquilinum	1500	SF	0.8	0.011
Pteris orizabae	1500	DF	0.8	0.014
Scoliosorus ensiformis	2000	NF	0.8	0.008
Selaginella stellata	2000	NF	1	0.003
Selaginella silvestris	2500	SF	1	0.002

Tectaria heracleifolia	500	NF	0.947	0.004
Terpsichore asplenifolia	1500	NF	0.8	0.01
Thelypteris dentata	1500	DF	0.6	0.049
Thelypteris rudis	1500/2000	SF	0.666/0.823	0.002/0.002
Vittaria gramminifolia	1500/2000	NF	1.000/0.628	0.003/0.029